Individual patterns of prey selection and dietary specialization in an Arctic marine carnivore

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The cumulative effect of individual-level foraging patterns may have important consequences for ecosystem functioning, population dynamics and conservation. Dietary specialization, whereby an individual exploits a subset of resources available to the rest of the population, can develop in response to environmental or intrinsic population factors. However, accurate assessment of individual diets may be difficult because analyses of recent food intake may misrepresent foraging variability within a heterogeneous environment. We used quantitative fatty acid signature analysis (QFASA) and a novel index of longitudinal dietary change to examine the individual foraging patterns of 64 polar bears *Ursus maritimus* successively sampled in Western and Southern Hudson Bay between 1994–2003. Estimated diets varied between and within age and sex classes, with adult male polar bears consuming significantly more bearded seal *Erignathus barbatus* than adult female or subadult bears, whose diets were dominated by ringed seal *Pusa hispida*. Among individual adult males, consumption of bearded seal accounted for 0–98% of the diet and bearded seal consumption was positively correlated with individual dietary specialization, as measured by proportional similarity (PS_i) to the rest of the population. Most individual diets were consistent from year-to-year and were therefore not a product of short-term heterogeneity in prey distribution. However, a novel dietary change index indicated that adult male polar bears had the most temporally variable diets with 23% of adult males switching their diet from predominantly ringed seal to predominantly bearded seal or vice versa. We conclude that QFASA is well-suited to analyses of individual-level foraging because it reflects an animal's diet over the preceding weeks to months. The subpopulations of bears in this study were near the southern limit of their species range and have experienced negative individual- and population-level impacts related to sea ice loss and climate warming. The tightly constrained diets of some individuals, particularly adult females and subadults, may make them especially sensitive to future climate change.

Although prey selection occurs at the level of the individual, the cumulative consequences of individual predator–prey interactions have population and ecosystem-level effects (Krebs 1994). Optimal foraging theory predicts that individuals should adopt the strategy that maximizes the net rate of energy intake (MacArthur and Pianka 1966, Stephens and Krebs 1986). Given that all individuals in a predator population may have similar access to prey, the optimal diet in an energetic sense could be characteristic of the population. However, individuals differ in body size, growth rate, movement patterns, and reproductive status and as a consequence, the caloric requirements and foraging opportunities of individuals will probably vary within a population. Previous studies have identified intraspecific patterns of foraging that reflect age- and sex-specific differences in space use (Clutton-Brock et al. 1987, Wielgus and Bunnell 1995), energetic requirements (Clutton-Brock et al. 1987), hunting ability (Birks and Dunstone 1985), and diet selectivity (Houston and Shine 1993).

Dietary specialization, whereby an individual has a dietary niche that is either narrower than the population's niche or shifted to other resources to reduce niche overlap (reviewed by Bolnick et al. 2003, Sargeant 2007), has been observed in birds (Partridge 1976, Woo et al. 2008), fish (Schindler et al. 1997), mammalian carnivores (Estes et al. 2003, Tinker et al. 2008) and herbivores (McEachern et al. 2006). Individual patterns of foraging can develop for a number of reasons including a response to intraspecific competition (Schindler et al. 1997, Tinker et al. 2008), the need to learn complex foraging behaviour (Partridge 1976, Estes et al. 2003), or spatiotemporal variability in the distribution of resources (Woo et al. 2008). Individual foraging strategies may be maintained over time (Schindler et al. 1997) and even transferred to dependent offspring (Estes et al. 2003).

The highly seasonal distribution of resources in Arctic environments can result in strong trophic interactions (Post et al. 2009). Highly specific food and habitat requirements make large mammals in Arctic ecosystems vulnerable to

rapid, unidirectional, environmental change (Laidre et al. 2008). Yet few studies have attempted to quantitatively determine the extent to which individual dietary specialization may occur in Arctic mammals (but see Angerbjörn et al. 1994). Throughout their circumpolar range, polar bears *Ursus maritimus* feed predominantly on ringed seals *Pusa hispida* and to a lesser degree on bearded seals *Erignathus barbatus* (Stirling 1974, Stirling and McEwan 1975, Thiemann et al. 2008a). The abundance of polar bears and ringed seals in particular are highly correlated (Stirling and Øritsland 1995). However, because of large scale variability in the annual production and survival of ringed seal pups, their availability to polar bears can vary substantially between years (Smith and Stirling 1975, Stirling et al. 1982, Stirling 2002, 2005). In areas where a greater diversity of marine mammals occurs, polar bears may feed on a wider variety of species (Derocher et al. 2002, Iverson et al. 2006, Thiemann et al. 2008a), which differ in their relative abundance, ease of capture, and energetic content. However, little is known about the importance of secondary prey types or the intrinsic (e.g. age, sex) or extrinsic factors (e.g. sea ice conditions) that influence prey selection.

Analytical techniques based on the trophic transfer of fatty acids (FAs) have provided new insights into the foraging habits of free-ranging animals (reviewed by Budge et al. 2006, Iverson 2009). Because carnivores have strict biochemical limitations on FA synthesis, dietary FAs are predictably incorporated into, and can be identified within, the adipose stores of a predator. By comparing the FA profile of a predator with those of its potential prey and accounting for patterns of predator metabolism, quantitative FA signature analysis (QFASA) can generate estimates of the diet composition of individual animals. QFASA has been applied to seals (Iverson et al. 2004, Beck et al. 2007), seabirds (Iverson et al. 2007), and polar bears (Iverson et al. 2006, Thiemann et al. 2007, 2008a) and although it provides information on individual diets, to date these estimates have mainly been pooled to examine cross-sectional variability within (Beck et al. 2007) or among populations (Thiemann et al. 2008a).

We determined the diet composition of individual polar bears captured multiple times in Hudson Bay to examine several hypotheses: (1) Because the largest polar bears are able to capture the widest range of prey, as well as to kleptoparasitize smaller conspecifics (Stirling and Derocher 1990), we predicted that adult male bears (which are roughly twice the size of adult females; Kingsley 1979) would have the most temporally variable diets because they have a greater capability to adjust their foraging patterns to match local fluctuations in prey. (2) Because of their smaller size, subadult bears may be restricted to capturing smaller prey. We therefore predicted they would have less diverse and less variable diets than adult males. Alternatively, it is possible that subadults depend to an unknown degree on scavenging the remains of prey killed by larger bears and therefore might still show high temporal variability in diets. (3) Adult females accompanied by cubs tend to avoid adult males and, in many areas, focus their foraging activity on the stable land-fast ice, or large stable areas of offshore pack ice, where ringed seals haul out and breed (Stirling et al. 1993). Thus, we hypothesized that females with dependent cubs would have the least variable diets.

(4) Because solitary adult females forage in the same areas as adult males and may kill juvenile members of large-bodied species (e.g. bearded seals) as well as scavenge prey remains, we predicted that the annual variability in the diet of solitary adult females would be intermediate between that of adult males and females accompanied by cubs.

Methods

Sample collection and analysis

Polar bears were captured on land during capture-recapture studies in northeastern Manitoba and northern Ontario (Fig. 1). We conducted capture work in the fall (August–October) from 1994 to 2003 except 1997 and 1999. Bears were located from a helicopter and immobilized with Telazol delivered via remote injection (Stirling et al. 1989). At first capture, bears were assigned a unique identification number (e.g. X03331) which was tattooed on the inside of the upper lip and engraved on white plastic tags attached to each ear. Bears captured as cubs-of–the-year were known age. The age of older bears was determined by counting cementum annuli in a vestigial premolar tooth (Calvert and Ramsay 1998). Bears $\geq$ 5 years were considered to be adults and those 3–4 years were classified as subadults.

To focus on temporal variability and control for ontogenetic shifts in diets, we only included in the study those bears that were captured multiple times while still in the same age class. Consequently, most bears were adults, although three bears were captured twice as subadults. Similarly, to control for the possible influence of reproduction, we only included those females that were captured multiple times either with or without cubs.

We estimated diets from the FA composition of polar bear adipose tissue which we sampled as a tissue biopsy from each animal at every capture. Tissue samples were taken through the skin on the rump of the bear approximately 15 cm lateral to the base of the tail; this subcutaneous fat depot is the largest and expands the most rapidly with changes in body condition (Pond et al. 1992), and its FA composition reflects that of the entire subcutaneous layer (Thiemann et al. 2006). Tissue samples were stored in air-tight containers and kept frozen (–20°C) until laboratory analyses were completed (generally < six months). All immobilization and live-capture procedures were reviewed and approved annually by the Animal Care Committee of the Canadian Wildlife Service, Prairie and Northern Region, Edmonton, AB and by the Animal Care Committee of the Ontario Ministry of Natural Resources, Peterborough, ON.

We determined the FA composition of each biopsy by quantitatively extracting the lipid using a Folch extraction (Folch et al. 1957) as modified by Iverson et al. (2001). FA methyl esters were prepared using H_2SO_4 as a catalyst (Budge et al. 2006) and analyzed in duplicate on a gas chromatograph fitted with a flame ionization detector and a flexible fused silica column (30 m $\times$ 0.25 mm ID) coated with 50% cyanopropyl polysiloxane (0.25 μm film thickness). FAs were measured as the mass percent of all FAs in the extracted lipid sample.
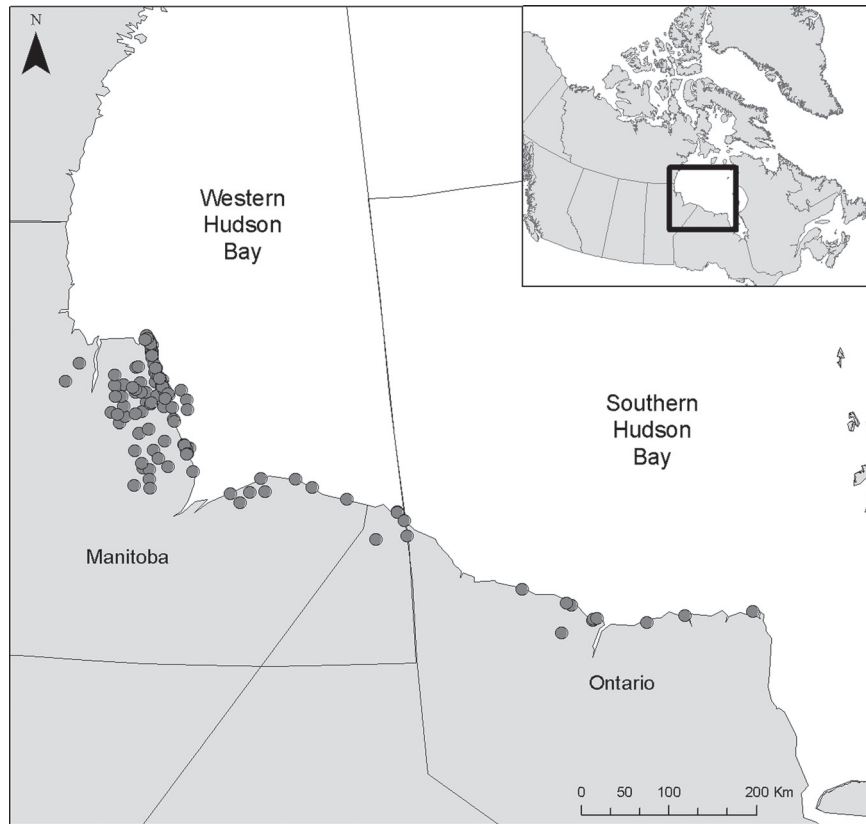
Figure 1. Location of 143 captures of polar bears in the Western Hudson Bay and Southern Hudson Bay subpopulations. Diets were estimated from the fatty acid composition of adipose tissue samples collected from 64 bears captured two to five times each between 1994 and 2003.

Quantitative fatty acid signature analysis (QFASA)

We estimated polar bear diets using the QFASA modeling technique developed by Iverson et al. (2004, 2006) and the marine mammal database, calibration coefficients, and FA set established by Thiemann (2006) and Thiemann et al. (2008a). Briefly, polar bear FA signatures were calibrated to account for FA-specific patterns of metabolism within the predator using calibration coefficients (Iverson et al. 2004) developed from studies on captive mink *Mustela vison* (Thiemann 2006). The combination of prey FA signatures that came closest to matching the observed calibrated polar bear profile was then determined, thereby estimating diet (Iverson et al. 2004).

We modeled polar bears in this study using a database of prey FA signatures developed from blubber samples of ringed seal (n = 52), bearded seal (n = 12), harbour seal *Phoca vitulina* (n = 33), harp seal *Pagophilus groenlandicus* (n = 239), and beluga whale *Delphinapterus leucas* (n = 28). Prey samples were collected in Hudson Bay, or in the case of harp seals, in the Labrador Sea (Thiemann 2006). The QFASA model generated an estimated diet for each polar bear sample that reflected the relative amount of prey biomass consumed (rather than the number of prey animals killed). Average prey signatures were input in the model and therefore the individual diet estimates presented here do not incorporate the FA variability present within a prey

species. Previous studies (Thiemann 2006, Thiemann et al. 2008a) used a bootstrapping procedure (Iverson et al. 2004) to capture the variability in both prey FA and predator diet estimates (Beck et al. 2007). However, because intraspecific variability in marine mammal FA is small relative to inter-specifc differences (Thiemann et al. 2008b), inclusion of within-prey variability has little impact on polar bear diet estimates (Thiemann 2006, Thiemann et al. 2008a).

Dietary niche breadth was calculated for each sampling event using the Shannon–Wiener index (H'; Krebs 1994):

$$H' = -\sum_{j=1}^{S} p_j \ln p_j$$

where p_j is the proportion of prey species j in the diet and S is the total number of prey species consumed by all polar bears. We also used IndSpec1 (Bolnick et al. 2002) to calculate the proportional similarity index for each individual i (PS_i) and the mean proportional similarity across the population (IS). PS_i quantifies individual specialization by measuring the overlap between an individual's diet and that of the population (Feinsinger et al. 1981, Bolnick et al. 2002). Therefore, the most specialized individuals (i.e. those with the lowest PS_i) have diets that are the most distinct from the rest of the population. Because individual polar bears were sampled repeatedly over time, we used linear mixed models to test for intra-population differences in diet composition, dietary

diversity (H') and proportional similarity (IS) between groups. Proportional diet and PS_i data were arcsine-square root transformed prior to testing (Zar 1999).

Cross-sectional age- and sex-specific variability in polar bear diets were examined by Thiemann et al. (2008a). In the current study, we were interested in quantifying the degree to which individual diets varied over time. To this end, we developed a novel dietary change index (DCI) for each polar bear as follows:

$$DCI = \sum_j \left(\frac{\sum_{y-1} \left| p_{jt} - p_{jt-1} \right|}{y-1} \right)$$

where p_{jt} is the proportion of prey type j in the diet of a bear sampled in year t, and y is the number of different years in which the bear was captured. The DCI represents the sum of the average annual change in the proportion of each prey and its value ranges from 0 (no change in diet) to 2 (complete replacement of all original prey). The maximum value of 2 is a consequence of using proportional data, where an increase in the consumption of one prey type must be accompanied by a corresponding decrease in the consumption of another. For our purposes, this simple index performed better than the χ^2 contingency tests within individuals used by Estes et al. (2003) because it was relatively insensitive to fluctuations in minor prey types. For instance, a dietary change from 90% ringed seal and 10% bearded seal to 90% ringed seal and 10% harbour seal would generate a highly significant χ^2-value but a fairly low DCI value of 0.20. Even a change from 90% ringed and 10% bearded seal to 90% ringed, 5% bearded, and 5% harbour seal would yield a significant χ^2-test at $\alpha = 0.05$ but a low DCI value of 0.10. We feel that the above hypothetical changes are less biologically important as only minor portions of the bear's diet were changing over time. Although the DCI does not incorporate the length of time passed between sampling events, it captures the temporal variability that is apparent in individual polar bear diets without overstating the importance of small annual changes. We used one-way ANOVA (SPPS ver. 17.0) to compare log-transformed DCI values across age and sex groups. Mean values are reported ± SE.

Results

In Western Hudson Bay, 59 polar bears were caught two to five times each for a total of 133 capture events between 1994 and 2003 (Fig. 2a). In Southern Hudson Bay, five polar bears were captured twice each between 2001 and 2003 (Fig. 2b). Because few bears were handled in Southern Hudson Bay and there were no a priori reasons to expect substantial differences in their foraging habits (Thiemann et al. 2008a), data from the two subpopulations were pooled for analysis. Adult females with cubs-of-the-year did not differ from females with older cubs in any foraging metric. There were also no differences between females accompanied by dependent young and those that were captured alone so all adult females were considered collectively in further analyses.

The diets of most individuals were dominated by ringed seal, but some adult male polar bears consumed large proportions of bearded seal (Fig. 2); in 33 cases (all of which were adult male bears), bearded seal accounted for > 40% of the diet. Harp seal, harbour seal, and beluga whale were minor dietary components although one adult male (X17076) obtained more than 45% of its diet from harbour seal in 2003 and another adult male (X10857) consumed more than 44% harp seal in 2000. A trace amount of beluga whale (<1%) appeared in the estimated diet of one bear (X16350) in 2003. On average, adult male polar bears derived a greater percentage of their diet from bearded seal (33%) than did adult females (12%; linear mixed model, p < 0.001) or subadult bears (8%; p = 0.004; Table 1). There was no significant difference in the proportion of bearded seal in the diets of subadults and adult females (p = 0.548). Bearded seal consumption by adult female and subadult polar bears never exceeded 38%, whereas among adult males, bearded seal accounted for up to 98% of an individual's diet. Such widely variable bearded seal consumption contributed to the greater dietary niche breadth of adult males ($H' = 0.79$) compared to other groups ($H' = 0.51$–0.65, linear mixed model: p < 0.004; Table 1).

Intra-population differences in PS_i values were not significant (p = 0.407) because of a strong non-linear relationship between PS_i and the proportion of bearded seal in the diet (Fig. 3); bears with the most generalized diets (i.e. PS_i close to 1) consumed intermediate proportions of bearded seal. Although relatively low PS_i values (indicative of specialization) were produced from some bears feeding almost exclusively on ringed seal (Fig. 3), above a threshold of ca 30% bearded seal consumed, dietary specialization increased with increasing consumption of bearded seal. Using PS_i values, bears consuming large amounts of bearded seal are more specialized because their diets are the most dissimilar to the population as a whole.

In addition to being the most individually specialized (i.e. lowest PS_i values; Fig. 3), the diets of adult males also tended to be the most variable over time. DCI values (Table 1, Fig. 4) indicated more temporal variably among adult males (0.52) than adult females (0.34; ANOVA, $F_{2,61} = 18.5$, Bonferroni p = 0.015) or subadults (0.09; Bonferroni, p < 0.001). Individual bears in this study were re-sampled one to four times each, but the number of repeat samples had no effect on a bear's DCI value (ANOVA, $F_{3,61} = 0.71$, p = 0.550). Although relatively few samples were available from adult female and subadult polar bears, the limited variability in the diet of adult females suggests that sex-specific trends were not influenced by sample size. However, trends in subadults should probably be interpreted cautiously.

Discussion

Prey selection patterns may be influenced by an individual's morphology, physiology, experience or behaviour and individual specialization can have important demographic impacts on a population (Bolnick et al. 2003). Among polar bears in Hudson Bay, patterns of prey selection, as well as dietary breadth and variability, differed among individuals. Adult male polar bears are capable of preying heavily
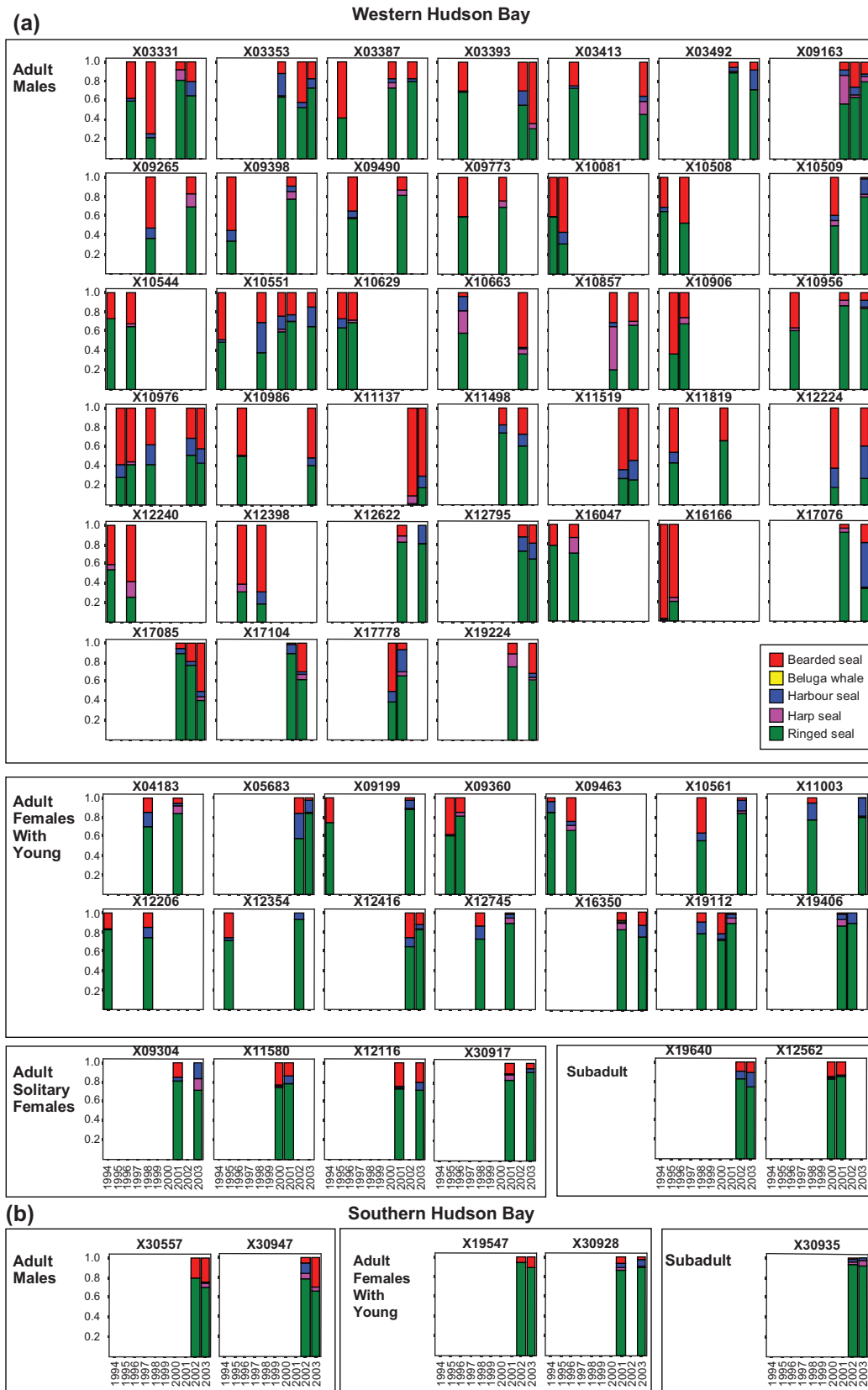
Figure 2. Diet composition estimated by QFASA for polar bears sampled multiple times in (a) Western Hudson Bay and (b) Southern Hudson Bay between 1994 and 2003 (except 1997 and 1999). Coloured bars indicate the proportional diet composition of an individual bear sampled in a given year. Longitudinal data for each individual are presented in small boxes labeled with the bear's unique identification number (e.g. X03331).

Table 1. Mean proportional diet composition, diversity (H'), proportional similarity (IS), and temporal variability (dietary change index, DCI) for polar bears in Hudson Bay. Diet composition was estimated for individual bears using QFASA. SEM in parentheses.

Group	Bears (n)	Samples (n)	Bearded seal	Beluga	Harbour seal	Harp seal	Ringed seal	H'	PS_i	DCI
Adult male	41	96	0.33 (0.02)	0.00 (0.00)	0.07 (0.01)	0.03 (0.01)	0.56 (0.02)	0.79 (0.02)	0.77 (0.01)	0.52 (0.04)
Adult female (with young)	16	33	0.12 (0.02)	0.00 (0.00)	0.08 (0.01)	0.02 (0.00)	0.79 (0.02)	0.61 (0.03)	0.80 (0.01)	0.36 (0.04)
Adult female (solitary)	4	8	0.14 (0.03)	0.00 (0.00)	0.06 (0.02)	0.03 (0.02)	0.78 (0.02)	0.65 (0.05)	0.83 (0.03)	0.26 (0.08)
Subadult	3	6	0.08 (0.03)	0.00 (0.00)	0.06 (0.02)	0.02 (0.01)	0.84 (0.03)	0.51 (0.06)	0.77 (0.02)	0.09 (0.04)

on bearded seals and some individual males could reasonably be called bearded seal 'specialists'. However, as a group, adult male bears also showed the greatest dietary flexibility as revealed by their broad and temporally variable diets. For instance, only adult males switched from one primary prey type to another (i.e. from predominantly ringed seal to predominantly bearded seal or vice versa). Of the 39 adult male polar bears sampled in Western Hudson Bay, nine (23%) made such a switch (Fig. 2). This dietary flexibility likely represents an important adaptation to the Arctic environment where the distribution of prey may be temporally and spatially variable. In contrast to adult males, subadult and adult female bears had narrower and less variable diets and thus appear to rely more heavily on the availability of ringed seals.

Their greater dependence on a single prey species may make adult females and subadults more vulnerable to climate-related changes in sea ice and associated declines in ringed seal availability (Ferguson et al. 2005, Stirling 2005). For example, declines in body condition in the Southern Hudson Bay subpopulation were greater for adult females and subadults than for adult males (Obbard et al. 2006). Observed declines in the abundance of Western Hudson Bay polar bears appear to have been driven by declines in female natality and reduced

survival rates of cubs, subadults, and old adults (Stirling et al. 1999, Regehr et al. 2007). This suggests that adult males may be better able to buffer effects of future changes in sea ice conditions, at least in the short term, due to their ability to exploit additional prey species. However, the relative resilience of adult males should not be expected to reduce the negative impacts of climate change on population vital rates.

Intra-population patterns of prey selection

Age- and sex-specific foraging patterns were consistent with known differences in polar bear hunting ability and energy requirements. Adult male polar bears are roughly twice the size of adult females, a pattern that likely evolved in response to intense male–male competition during the breeding season (Ramsay and Stirling 1986, Stirling and Derocher 1990) and which makes it physically possible for adult males to capture and kill larger prey, including adult bearded seals which may have a body mass up to 350 kg (Smith 1981). The greater dietary diversity (H') of adult male polar bears relative to other age and sex classes supports our hypothesis and is a predictable consequence of males consuming both bearded and ringed seals, whereas other bears were largely limited to preying on ringed seals.

In other size-dimorphic species, dietary diversity may be driven by less selective foraging in the larger-bodied group as these animals have greater absolute energy requirements and
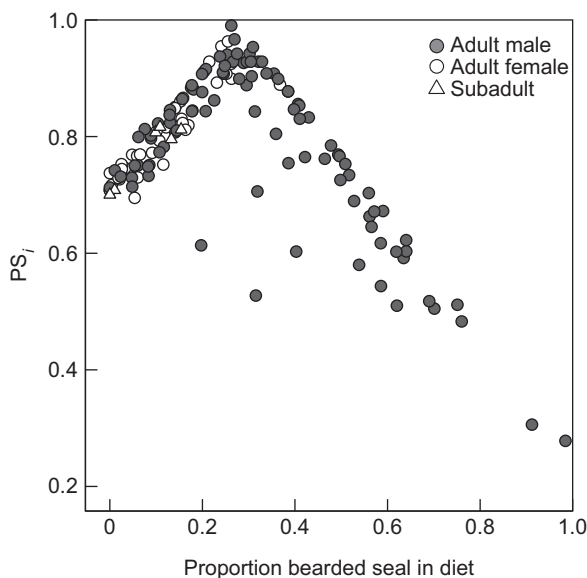

Figure 3. Proportional dietary similarity (PS_i) versus the relative consumption of bearded seal by individual polar bears in Western and Southern Hudson Bay. High PS_i values indicate high dietary overlap with the rest of the population whereas low values indicate dietary specialization.
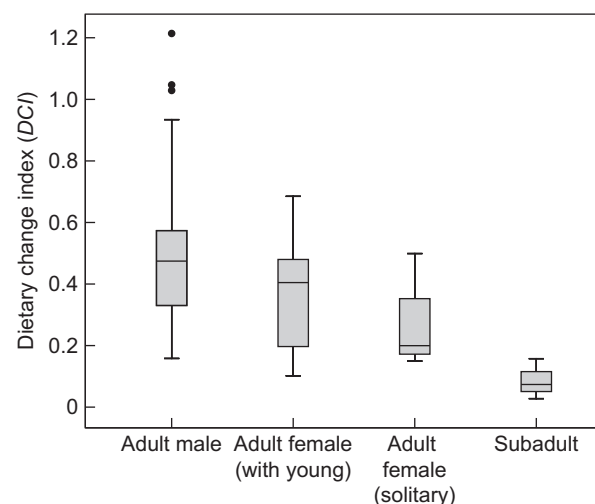

Figure 4. Dietary change index for polar bears of different age and sex classes in Western and Southern Hudson Bay. Lines in the boxes indicate the median and the 25th and 75th percentiles. Whiskers indicate 95% CI and points reflect outliers.

potentially greater tolerance for low-quality prey (Clutton-Brock et al. 1987, Beck et al. 2007). In polar bears, a lack of selectivity does not explain the broader diets of adult males, as some individuals consistently fed on bearded seals in multiple years (e.g. X10976, X11519; Fig. 2) and bearded seals could not be considered low-quality prey. Differences in foraging patterns may also arise from spatial segregation among intraspecific groups (Wielgus and Bunnell 1995) and adult female polar bears with cubs-of-the-year may avoid potentially infanticidal males by foraging in areas of stable landfast ice where male bears, and bearded seals, occur less frequently (Stirling et al. 1993). However, subadult bears and adult females without young cubs may use the same types of habitat as adult males and, in Hudson Bay, all groups of bears may overlap, as landfast ice is relatively sparse (Markham 1986, Lunn et al. 1997). We therefore suggest that intraspecific differences in polar bear foraging in Western and Southern Hudson Bay are driven more by sexual size dimorphism than by spatial segregation. Regardless of the proximate mechanism, dietary divergence within the population can reduce intraspecific competition for food (Kie and Bowyer 1999, Clarke et al. 1998).

In addition to their broader dietary diversity, adult male foraging habits were both the most individually specialized (PS_i) and temporally variable (DCI). Individual patterns of prey selection are discussed further below but, cumulatively, these results suggest that, because of their larger body size, adult males have more choice in selecting prey of different sizes and are therefore better able to exploit locally abundant or fluctuating prey. To further test this hypothesis would require additional data on seal abundance, productivity, and distribution in relation to annual variation in the diets and fitness of individual polar bears in Hudson Bay.

The relatively narrow but temporally consistent diets of subadults supports our hypothesis and suggests that these bears obtain the bulk of their dietary energy by actively preying on ringed seals, rather than scavenging the kills of larger bears. If carrion comprised a large portion of subadult diets, we would expect to see greater individual and temporal variability, and contributions from prey types other than ringed seal. However, it is also important to note that ringed seal carcasses may be more frequently available than any other carrion and FA analysis only quantifies the proportional intake of dietary lipids. Thus, the lean tissues of seal carcasses may still represent an important, yet unquantified, source of dietary protein for subadult polar bears.

A small sample size of solitary adult females limited our ability to test for the potential influence of dependent cubs on foraging by their mothers. Relative to adult males, females were less diverse, less specialized, and less temporally variable in their patterns of prey selection. We hypothesized that these foraging patterns would be even more restricted in females with associated young, but the lack of support for this hypothesis may be related to the limited availability of landfast ice refugia in Hudson Bay, which reduces the spatial segregation between females with cubs and adult males. Higher than expected dietary diversity and variability might also arise from family groups scavenging on diverse carrion.

Individual patterns of prey selection

Although 'individual foraging specialization' has various meanings and definitions in the literature, dietary specialists are those individuals that either (1) consistently use a subset of available resources and therefore have a narrower niche than the population as a whole, or (2) use different resources than other individuals and have a niche that overlaps little with the population niche (i.e. niche width vs niche overlap: reviewed by Sargeant 2007). We suggest that the feeding habits of adult male polar bears in Hudson Bay include both strategies. The few adult males that fed nearly exclusively on bearded seals had extremely narrow niches relative to the population, whereas those males that consumed intermediate levels of bearded seal effectively reduced niche overlap by exploiting a different resource than the rest of the population. According to the above definitions, bears consuming a substantial amount of bearded seal could be considered individual dietary specialists.

A number of factors could favor the development and maintenance of dietary specialization, including morphological (mainly size) differences in prey capture efficiency, individual patterns of space use, habitat preferences of prey, the influence of intra-and inter-specific competition, and individual learning. Although our data are limited to diet composition, we briefly explore how these factors may influence prey selection in individual polar bears.

Stirling and Derocher (1990) speculated that, although competition for mates appears to be the main reason for sexual size dimorphism in polar bears, being able to access larger prey may also have had an influence. Thiemann et al. (2007) found that among adult male polar bears, body size was positively related to bearded seal consumption. Our results suggest that morphological differences in prey capture ability (i.e. larger bears can catch larger seals) drive individual dietary specialization in polar bears. Bearded seals, by virtue of their larger size, offer a large energetic reward for those bears able to capture them. However, considering that not all adult males were bearded seal specialists and that polar bears exhibit complex hunting behaviour (Stirling 1974), the development of individual skills through learning, or cultural inheritance of hunting techniques specific to bearded seals, remains a possibility.

The habitat an individual occupies may also have a strong influence on its diet. For example, Angerbjörn et al. (1994) found that individual Arctic foxes *Alopex lagopus* occupying coastal territories consumed greater amounts of marine-based food than did individuals with less access to the sea. Likewise, individual adult female polar bears display tremendous variation in the size of their home ranges (from approximately 200 km² to >500 000 km²; Amstrup et al. 2000, Mauritzen et al. 2001) and use distinct space-use strategies whereby some individuals forage in offshore pelagic habitats whereas others show fidelity to small coastal areas (Mauritzen et al. 2001, Stirling unpubl.). Such variable behavioural strategies are likely associated with differences in both prey availability and the amount of energy that must be expended to exploit different niches. Such differences correspond well with our data.

Sea ice is dynamic and the abundance and distribution of ice-associated seals can change dramatically between years

(Stirling et al. 1982) and possibly over shorter periods. Our data suggest that despite this variability, individual polar bears may show fidelity to feeding areas that have some consistency in the availability of particular prey. For instance, near-shore coastal areas and fiords may have seasonally high densities of ringed seals (Smith and Stirling 1975) whereas bears foraging in the offshore pack ice will have greater access to bearded seals (Stirling et al. 1982, Lunn et al. 1997). In Hudson Bay, an extensive shore-lead system that limits the amount of landfast ice may also increase the seasonal predictability of sea ice habitat. As with polynyas in other parts of the Arctic (Stirling 1980), the Hudson Bay shore-lead system generates areas of open water that are predictable in time and space. Although variability in sea ice may make prey distribution unpredictable on short time-scales such as days, conditions across intermediate time-scales (i.e. weeks to years) probably allow individual polar bears in Hudson Bay to consistently target specific prey (see also Mauritzen et al. 2001). Further study of the spatial and temporal relationships between space-use, habitat selection, and foraging patterns would provide insight into the processes governing polar bear demography.

Estes et al. (2003) predicted that dietary specialization should be most common in food-limited apex predators where interspecific competition is weak and intraspecific competition is strong (Holbrook and Schmidt 1992, Svanbäck and Bolnick 2005). As top predators with no significant interspecific competition for prey, polar bears closely fit this model. Although density dependent processes are poorly understood in polar bears, intraspecific competition for ringed seals may promote resource partitioning and increase the fitness benefits for males specializing on bearded seals. Because at present bearded seals have no other large predators, they may represent an available niche for male bears.

Although the factors influencing prey choice in polar bears are not yet fully understood, their foraging patterns and demography in the Western Hudson Bay subpopulation appear to be correlated. Thiemann et al. (2008a) found that bearded seal consumption in Western Hudson Bay declined from more than 40% of dietary biomass in 1995 to only 15% in 2003. Over approximately the same period, the Western Hudson Bay subpopulation declined by about 22% (Regehr et al. 2007). How, or whether, changes in the availability of prey may have contributed to the decline in polar bears is uncertain, but the primary importance of 'alternate' or 'secondary' prey (i.e. species other than ringed seal) for some individuals should be considered when attempting to predict the ecological impacts of Arctic climate warming. Currently, little information is available on the movements or space use patterns of adult male polar bears, largely because of the difficulty of fitting males with telemetry collars. Our results indicate that a substantial proportion of adult males may use fundamentally different resources (and therefore possibly different habitats) than other bears. Habitat models based only on the movements of adult females may not fully represent the habitat preferences of all demographically important groups.

FA data are particularly well-suited to analyses of individual diets because they reflect an animal's integrated diet composition over ecologically relevant time-scales (i.e. weeks

or months, Iverson et al. 2004). Other methods that provide a 'snapshot' of the most recent food intake (e.g. stomach contents, scat analysis) may misrepresent individual variability in foraging in animals in a heterogeneous environment. For example, sampling an animal just after feeding in a patch dominated by a single food type could bias our understanding of the normal diversity in its diet. Thus, longitudinal study of individuals using tools such as QFASA is the most effective means of measuring dietary preferences (Bolnick et al. 2002).

To our knowledge, this is the first systematic analysis of individual foraging specialization in an Arctic marine carnivore and the possibility that individuals of other northern species specialize on specific prey warrants further study. Woo et al. (2008) found that Brünnich's guillemots *Uria lomvia* in Nunavut showed a greater degree of individual specialization than the average of 49 other taxa. Although they found no direct fitness benefits of being a specialist versus being a generalist, they speculated that the benefits of the two strategies may fluctuate with decadal-scale changes in prey availability. For polar bears, the survival or reproductive benefits of individual dietary specialization are unknown, but given that ringed seals may undergo rapid fluctuations in abundance (Stirling et al. 1982), dietary flexibility is likely advantageous. Our data suggest that, because of their tightly constrained diets, adult female and subadult polar bears may be particularly sensitive to near-term declines in habitat and prey availability. A recent modeling study projected rapid declines in the survival of Hudson Bay polar bears as a result of climate warming (Molnár et al. 2010). Because these projections were based on data from adult males, they likely represent a best-case scenario. Given the potential for rapid, non-linear declines in survival associated with ongoing sea ice loss in Hudson Bay (Stirling and Parkinson 2006, Regehr et al. 2007), quantifying the demographic effects of polar bear foraging patterns should be a research and conservation priority.

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